Diet shift in bank voles induced by competition from grey-sided voles?

Magnus Magnusson[1*], Gustaf Samelius[2,3], Birger Hörnfeldt[1], Frauke Ecke[1]

[1]Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden.

[2]Snow Leopard Trust, 4649 Sunnyside Avenue North, Seattle, USA

[3]Department of Ecology, Swedish University of Agricultural Sciences, 730 91 Riddarhyttan, Sweden.

* Corresponding author:

Address: Department of Wildlife, Fish, and Environmental Studies, SLU, SE-901 83 Umeå, Sweden

Email: magnus.magnusson@slu.se; Telephone no: +46(0)73 0215 266

ABSTRACT

Grey-sided voles (*Myodes rufocanus* Sundevall, 1846) and bank voles (*Myodes glareolus* Schreber, 1780) co-exist in boreal forests in northern Scandinavia. Previous studies suggest that the two species interact interspecifically, the grey-sided vole being the dominant species. We tested the hypothesis that bank voles shift their diet due to competition with the dominant grey-sided vole by studying stable isotope ratios in both species. Muscle samples were taken from voles in patches of old forest occupied by *only* bank voles and patches of old forest occupied by *both* grey-sided voles and bank voles. We found that (1) stable isotope ratios of bank voles differed in areas with and without grey-sided voles and that (2) the stable isotope ratios of bank voles were more similar to those of grey-sided voles in areas where grey-sided voles were absent. Our data suggests that grey-sided voles forced bank voles to change their diet due to interspecific competition.

Key words: Competition, Diet shift, *Myodes glareolus*, *Myodes rufocanus*, Stable isotopes

INTRODUCTION

Environmental conditions and available resources limit the fundamental niche of species, while symbiotic relationships, competition and predation form a species' realized niche (Hutchinson 1957; Begon *et al.* 2006). The classic theory of species co-existence and niche differentiation was developed using a two-species competition system (Volterra 1926; Lotka 1932; Tokeshi 1998). In recent literature, the importance of niche differences for

maintaining species diversity has been discussed (Levine & HilleRisLambers 2009). The realized dietary niche can shift between sites for different species suggesting that species may be able to adjust their diets to minimize foraging competition (Hamel *et al.* 2013; Baltensperger *et al.* 2015).

Prolonged interspecific competition can result in resource partitioning among species (Roughgarden 1976; Schoener 1983). By using stable isotope analysis to understand resource partitioning, Calandra *et al.* (2015) showed that the diet of arvicoline rodents was structured according to phylogeny. As a consequence of shared resources, interspecific competition between two related species, the Eurasian red squirrel (*Sciurus vulgaris* Linnaeus, 1758) and the alien grey squirrel (*Sciurus carolinensis* Gmelin, 1788), occurred when the food became limited (Wauters *et al.* 2002). Similarly, when food resources were plentiful, American mink (*Mustela vison* Schreber, 1777) became more generalistic in their diet to avoid competition with otters (*Lutra lutra* Linnaeus, 1758) (Clode and Macdonald 1995).

Food supply is also an important predictor of reproductive success of most microtine rodents (Koskela *et al.* 1998). Generally, microtine rodents tend to be limited by food and have a low-quality food diet (Ostfeld 1985). As food is of such importance for the ecology of microtine rodents, it is crucial to get a better understanding if interspecific competition leads to changes in diet.

In boreal forests of northern Sweden, bank voles (BVs) and grey-sided voles (GSVs) co-exist. The GSV is the larger (Henttonen *et al.* 1977) and dominant species (Johannesen *et al.* 2002). Consequences for BVs when co-existing with the GSV are poorly understood but female GSVs may limit the breeding density of BVs (Löfgren 1995) and habitat selection

of the BV is affected by the presence of GSVs (Johannesen & Mauritzen 1999). Expected negative effects on demography parameters such as survival and recruitment of BVs due to interaction with the GSV were investigated in south-central Norway but no effect was found (Johannesen 2003). In contrast, red-backed voles (*Myodes rutilus*), a closely related species to the BV that occupy a similar ecological niche in the sub-Arctic small mammal community, was kept at low densities due to interspecific competition from the dominant GSV (Viitala 1984).

Stable isotope analyses have been used widely in ecological studies to study spatial and temporal variability in diet (Dalerum & Angerbjörn 2005; Baltensperger *et al.* 2015; Ehrich *et al.* 2015) and are based on the fact that stable isotope ratios in animal tissues reflect those of their food (Hobson 1999; Kelly 2000). The objective of this study was to investigate whether competition with the larger and more dominant GSV affected the diet of the BV. As a proxy, we examined differences in the diet of BVs by comparing stable isotope ratios ($\delta^{13}C$ (‰) and $\delta^{15}N$ (‰)) in BV muscle tissues in areas with and without GSVs. We also examined stable isotope ratios of the GSVs for similarities in diet between the two species. Stable isotope ratios reflect diet assimilated over time and vary between tissues in relation to their metabolic turn-over rate (DeNiro & Epstein 1978). Stable isotope signatures therefore reflect relatively long-term dietary composition when compared to traditional methods of estimating dietary composition such as stomach and scat content (DeNiro & Epstein 1978).

MATERIALS AND METHODS

Study area and vole samples

This study was conducted in the inland of Västerbotten County in northern Sweden in late September and October 2010 (Figure 1). We collected 20 grey-sided voles (GSVs) and 40 bank voles (BVs) by snap-trapping in eight study areas following the methods used within the National Environmental Monitoring Program (Hörnfeldt 1978, 1994, 2004; Ecke 2018). Twenty of the BVs were collected in study areas where there were no GSVs whereas the remaining BVs were collected in study areas where they coexisted with GSVs (Magnusson *et al.* 2013). All study areas were within patches of old coniferous forest of moist and mesic type (Arnborg 1990). The study areas with GSVs were generally characterized by many boulders and a dominance of old Scots pine trees (*Pinus sylvestris*; see detailed information on habitat requirement of GSVs in Magnusson *et al*. 2013). The field layer in all study areas contained a high proportion of ericoid dwarf shrubs. We did a vegetation inventory one year later than the vole trappings, in late September and October 2011. We do not expect the vegetation cover to change radically in a year in old boreal forests. We measured the cover of bilberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-ideae*), grasses, ground lichens, tree lichens and mosses in ten quadratic plots, with 2.5 m sides, 10 m apart and centered on the 10 trap-stations in the transect located in each study area. The cover was measured according to a 5-graded scale: 1 = 0 %; 2 >0 – 12 %; 3 >12 – 25 %; 4 >25 – 50 %; 5 >50 % (See detailed information of the vegetation inventory in Magnusson *et al.* 2013).

Study species

BVs and GSVs are forest living species: the GSV is a habitat specialist, preferring boulder rich old pine forest (Magnusson *et al.* 2013), while the BV is a habitat generalist occurring in many habitat types but with higher winter survival in old forests (Ecke *et al.* 2002; Savola *et al.* 2013). Ericoid dwarf shrubs (within the family Ericaceae) are important food for GSVs (Kalela 1957; Soininen *et al.* 2013), especially bilberry in autumn and winter (Hansson & Larsson 1978; Dahlgren *et al.* 2007). The BV also prefers to eat mature *Vaccinium*-berries in late summer and autumn (Hansson & Larsson 1978), a time of the year when BVs are mostly herbivorous (Hansson 1985). Seasonal variation in food abundance also results in a shift towards fruticose arboreal lichens in winter for BVs (Hansson 1985; Viro & Sulkava 1985; Ecke *et al.* 2018).

Stable isotope analyses

The metabolic turn-over rate of muscle is about one month (Hobson 1999), so stable isotope signatures of the vole tissues in our study thus represented the diet in late August and September since the voles were collected in late September and October. Stable isotope analyses were performed by the Stable Isotopes in Nature Laboratory (SINLAB) at University of New Brunswick in Canada and were performed using Continuous Flow Isotope Mass Spectrometry (CFIRMS) technology. Stable isotope ratios are expressed in δ-notation as parts per thousand (‰) deviations (see equation in Kelly 2000) from Peedee Belemnite (PDB; $\delta^{13}C$) and atmospheric air ($\delta^{15}N$). PDB is the international carbon isotope standard based on the fraction of heavy and light isotopes in marine fossils from the Peedee

limestone formation in South Carolina (Craig 1957), while atmospheric nitrogen is the standard for nitrogen (Ehleringer & Rundel 1989). For most tissues of plants and animals the $\delta^{13}C$ value is negative due to lower $^{13}C/^{12}C$ ratio than PDB and positive for $\delta^{15}N$ due to a higher ratio of 15N/14N than the atmospheric nitrogen standard (Kelly 2000).

Statistical analyses

We examined whether stable isotope ratios of BVs differed between areas with and without GSVs by a MANOVA (Proc GLM, SAS Institute Inc. 1990, n = 40 BVs from 8 study areas). In addition, to examine specifically for differences in $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) respectively for BVs in areas with and without GSVs, we used two general linear models (SAS Institute Inc. 1990, n = 40 BVs). We also examined whether the isotopic signatures of GSVs differed between the four study areas they occurred on by performing a MANOVA (Proc GLM, SAS Institute Inc. 1990; n = 20 GSVs). Similarly by using two separate MANOVAs, we also examined whether the isotopic signatures of BVs differed between the four study areas with GSVs (n = 20 BVs), and if the isotopic signatures of BVs differed between the four study areas without GSVs (n = 20 BVs). We used Mann-Whitney U-tests (TIBCO Software Inc.) to investigate whether study areas with GSVs and BVs differed from study areas with *only* BVs regarding mean cover of bilberry, cowberry, grasses, tree lichens, ground lichens and mosses.

RESULTS

Stable isotope ratios **(**and thus diet**)** of bank voles (BVs) differed between areas with and without grey-sided voles (GSVs) ($F_{2,37} = 21.16$, $P < 0.001$, Figure 2). More specifically, the difference was significant for $\delta^{13}C$ ($P < 0.0001$) but not for $\delta^{15}N$ ($P = 0.23$). During co-existence, stable isotope ratios of BVs were more different from those of GSVs than when BVs were alone (Figure 2). Moreover, stable isotope ratios differed between study areas for GSVs ($F_{6,30} = 16.25$, $P < 0.001$) and BVs from areas with GSVs ($F_{6,30} = 5.14$, $P = 0.001$) and without GSVs ($F_{6,30} = 12.03$, $P < 0.001$). GSVs from the same study areas showed similar patterns in stable isotope ratios, as did BVs mostly (Figure 3).

We did not find any statistical difference in mean cover of bilberry ($P = 0.5$), cowberry ($P = 0.8$), tree lichens ($P = 0.7$), or mosses ($P = 0.2$) between study areas with and without GSVs. However, there was a larger mean cover of ground lichens in study areas with GSVs ($P < 0.05$) while grasses were more common in study areas from whichGSVs were absent ($P < 0.05$).

DISCUSSION

Analyses of stable isotope ratios have been used widely in ecological studies, based on the fact that the ratios reflect those of the species' food (Hobson 1999; Kelly 2000). In this study, we found that the stable isotope ratios of bank voles (BVs) were different on study areas with grey-sided voles (GSVs) compared to areas without GSVs. The stable isotope ratios of BVs shifted away from those of the GSV when the species co-existed. We suggest

that the change in isotope ratios of the BVs was caused by competition with GSVs, forcing BVs to change their diet when coexisting with the larger and more dominant species. Similar type of diet shifts, likely caused by competition and food resources, have been found in other species systems (e.g Werner & Hal 1976; Alatalo *et al*. 1985; Clode & Mcdonald 1995).

Normally, the diet of the two species contain a high proportion of ericoid dwarfs shrubs (Hansson & Larsson 1978; Dahlgren *et al.* 2007; Soininen *et al.* 2013). Ericoid dwarf shrubs were common in all of our study areas and we did not find any difference in ground cover of either bilberry or cowberry between study areas with and without GSVs. However, we found a difference in the cover of grasses and ground lichens between areas with and without GSVs. Grasses were more common in areas with *only* BVs but since the BVs ate food that was more similar to GSVs in those areas than in areas where they co-existed (Figure 2), it is unlikely that grasses were responsible for the change in diet. Ground lichens were more common in areas with GSVs but like grasses, they are not the preferred food items of either GSVs or BVs (Hansson & Larsson 1978; Hansson 1979; Viro & Sulkava 1985). Therefore, we believe it to be unlikely that the voles competed for feeding on ground lichens or grasses. Anyway, we suggest that the diet shift was caused by food competition, maybe for bilberry, although we cannot yet pinpoint how the difference in $\delta^{13}C$ have arisen.

We do not know the stable isotope ratios of the potential food of the voles and therefore not the different food types consumed by the voles. However, the difference in $\delta^{13}C$ between

BVs with and without GSVs, may be linked to a difference in the isotopic signature of the different plants that the animals consumed (Kelly 2000). For example, lichens and fungi generally have high δ^{13}C-values (Calandra *et al*. 2015). As BVs also consume lichens, especially arboreal lichens in trees (Hansson 1985; Viro & Sulkava 1985), BVs may have higher δ^{13}C-values in areas with GSVs if they due to competition from GSVs shift their food from bilberry to lichens. However, the variation in the isotopic space is large for all plant types (Calandra *et al.* 2015) making any explanation of the difference in δ^{13}C for BVs in areas with and without GSVs mainly speculative. A removal experiment, removing GSVs from BV sites, while studying the diet of BVs would provide further insight into a potential competitive diet shift. Our study design did not allow for such experimental manipulation.

Our result suggesting a diet shift for BVs when coexisting with GSVs is novel, as previous studies on competition between the two species have either been looking at space use (Löfgren 1995; Johannesen & Mauritzen 1999), or dominance interactions due to size and aggressiveness in so called dyadic encounters (Johannesen *et al.* 2002). Our study thus adds further information on interspecific interactions between these microtine rodents. We suggest that future research should focus on gaining a better understanding of diet shifts induced by competition, preferably by using stable isotope analyses and, if possible, removal experiments. In addition, more studies of how diet shifts differ with seasonal variation in food availability are needed.

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FIGURE LEGENDS

Figure 1. Study areas in Västerbotten county, northern Sweden. (a) Four study areas where *both* GSVs (*Myodes rufocanus*) and BVs (*Myodes glareolus*) occurred (black circles) and four study areas were *only* BVs occurred (white circles); (b) Each study area was situated within a patch of old forest and (c) contained a 90 m long transect with 10 trap stations where (d) five snap-traps were placed within 1m from the circle center.

Figure 2. Variation in stable isotope signatures (measured by δ15N (‰) and δ13C (‰) in muscle tissues) for GSVs (*Myodes rufocanus*; black triangles) and BVs (*Myodes glareolus*; circles) at study areas with GSVs (black circles) and without GSVs (light grey circles).

Figure 3. Spatial variation in stable isotope signatures (measured by δ15N (‰) and δ13C (‰) in muscle tissues) for BVs (*Myodes glareolus*; circles) and GSVs (*Myodes rufocanus*; squares) at study areas where both species occurred. Voles from Norrgravsjö shown in white, Storberget in black and other areas (Trehörningen and Brandbärsberget) in light grey.

Figure 1

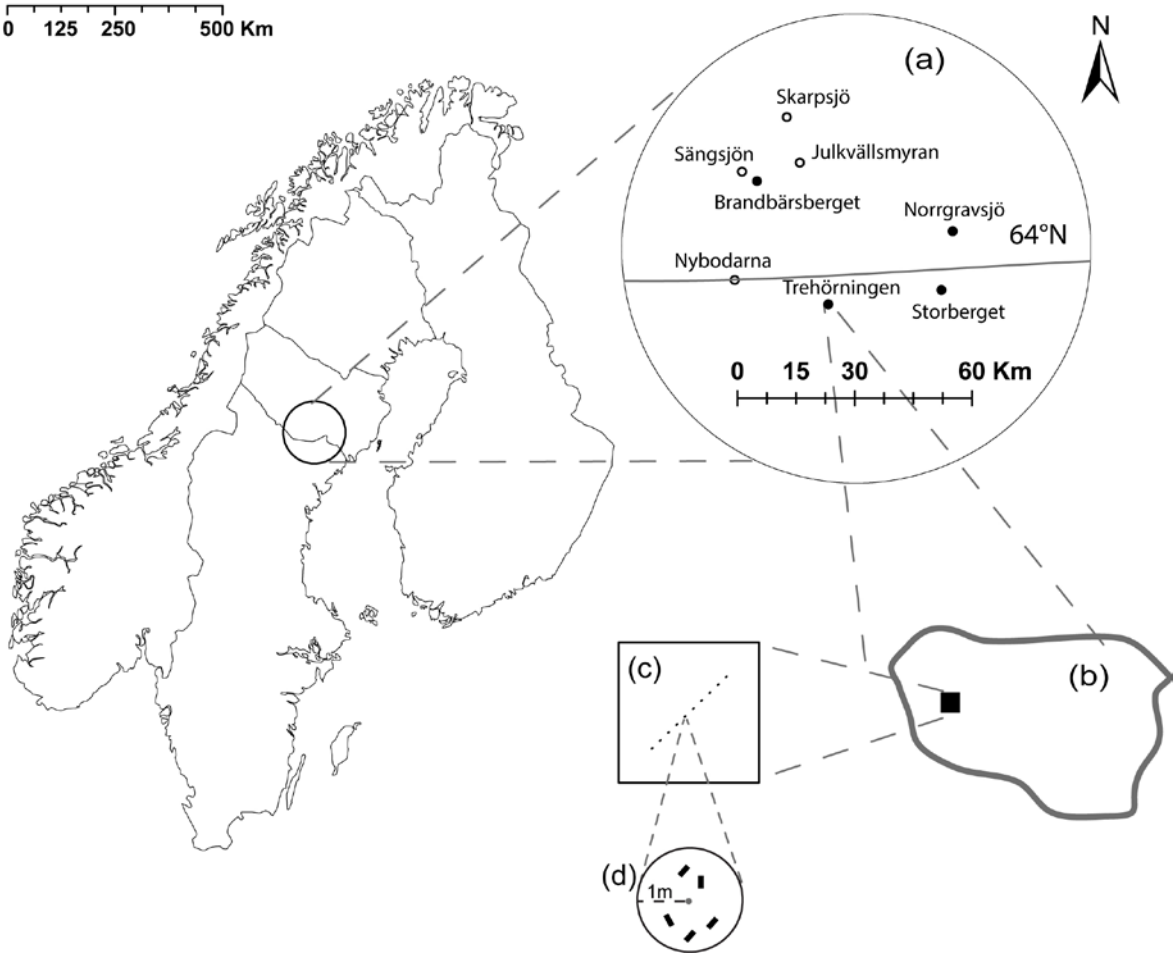
0 125 250 500 Km
N
(a)
Skarpsjö
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Figure 2

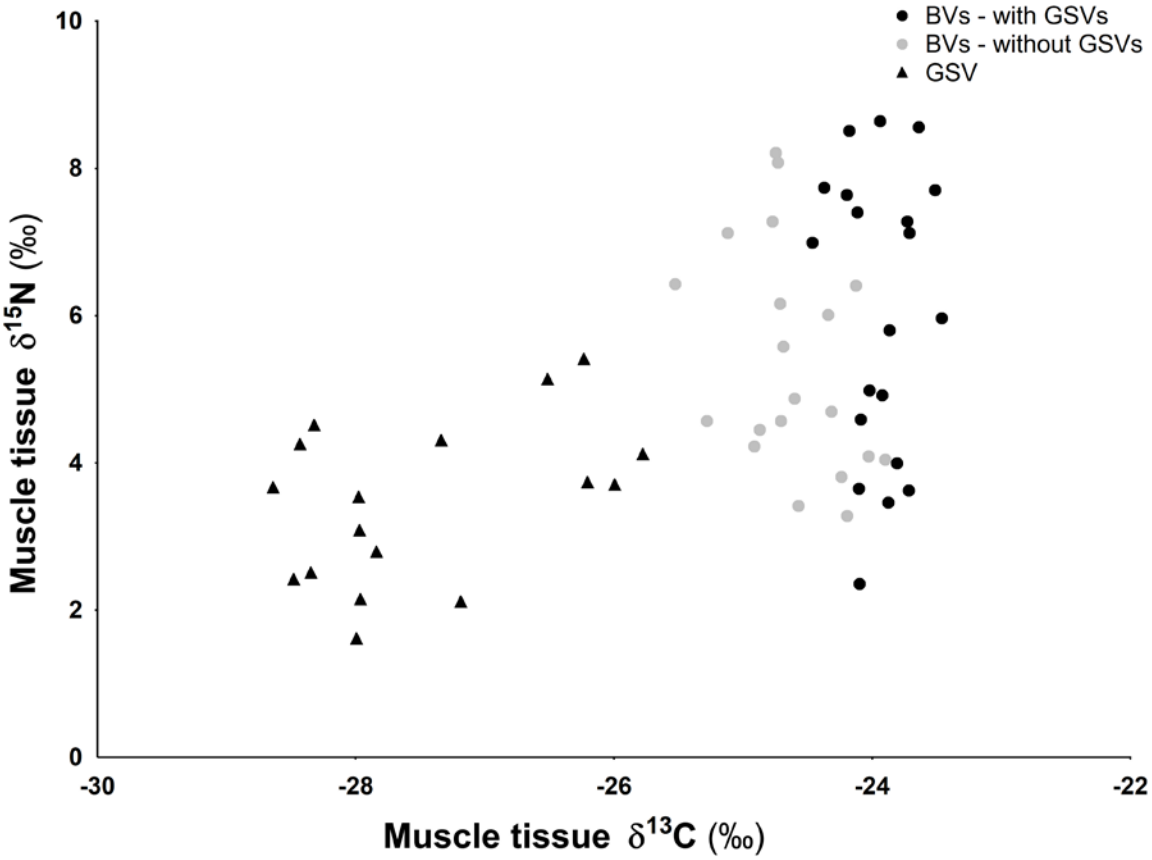
BVs - with GSVs
BVs - without GSVs
GSV
Muscle tissue δ15N (‰)
Muscle tissue δ13C (‰)
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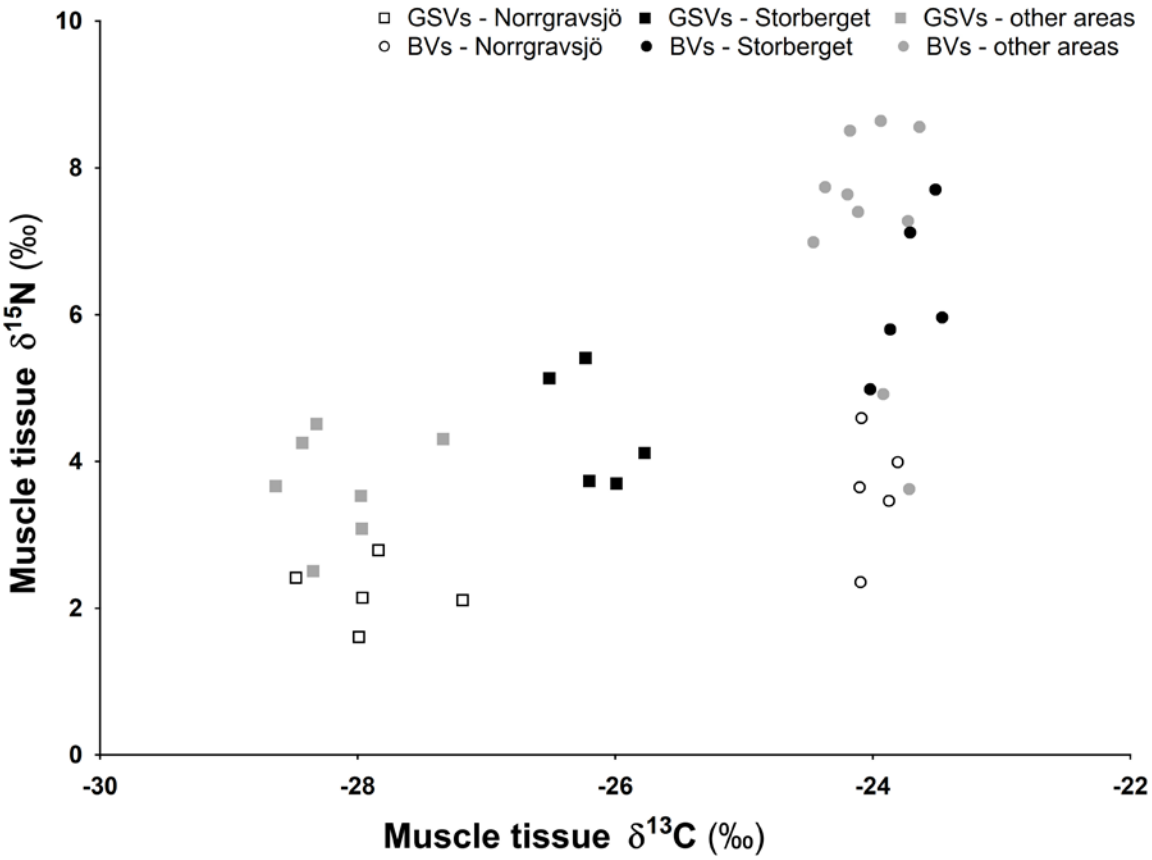
Figure 3


GSVs - Norrgravsjö
GSVs - Storberget
GSVs - other areas
BVs - Norrgravsjö
BVs - Storberget
BVs - other areas
Muscle tissue δ15N (‰)
Muscle tissue δ13C (‰)
10
8
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